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F. E. Alekseev

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THE THEORETICAL ASSUMPTIONS AND METHODS FOR INVESTIGATING COMMERCIAL FISH POPULATIONS

F. E. Alekseev

The broad formulation of the problem concerning the structure /5* of stocks of commercial fish is related to the work of F. Heincke [48], in which it was shown that a species is divided into intraspecific units - races. The races possess a definite distinct character, on the basis of which they become accessible to differential study. Their characterization includes geographic identification, common reproductive unity (kinship), and their individualism - i.e. the characteristics of the population as presently conceived. But the methods of division were purely morphological and the races themselves clearly proved to be units of different ranks.

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A general conception of the biological essence of intraspecific units was formulated during the on-going development of a theory of species from the typical conception of the Linnean monotypical species through the polytypical morphological species of Semenov-Tyan-Shanskii to the population and biological conception of Dobzhanskii and Mayr.

The typological conception considered the species as an /6
undivisible whole and by its very nature did not assume the existence of intraspecific groupings. With the formulation of the polytypical standard of the species, the question arose of its compatibility with notions of reality and of the unity of the species. Charles Darwin expressed doubt about the reality of the species [19], because he did not see any differences in in principle between mutants (which gave birth to species) and the species themselves. A. S. Semenov-Tyan-Shanskii [32] believed in the notion of the reality and the completeness of the species together with its subdivision (species - subspecies - tribe - morph - aberration). The subsequent discussion about the limits, the completeness, and the reality of the species did not reflect a "correct" or "incorrect" understanding of these problems so much as it reflected the complexity and the inconsistency that exists within a species which is evolving and the combination of integrating and differentiating factors that were operating simultaneously within its confines. The heart of the problem was the criteria of completeness and the reality of the species. Partisans of the polytypical conception appealed primarily to the morphological (morpho-physiological) unity of the species and to the hiatus between species. V. L. Komarov approached the problem from a completely different angle. He considered functional unity - "the common character of breeding

life" [13] - as the criterion for completeness; "the species is not a system, but an individual organism that is isolated during the process of evolution" [4]. The recognition of the monotypical species within the scope of a geographic race as an objective fact follows from this. Without references to the general evaluation of the views held by V. L. Komarov on the question of species, it should be noted that the formulation of the problem of functional unity as a criterion for the completeness of a species remains current to this day. The basis for a systematic organization of the polytypical species has been linked to the work of N. I. Vavilov entitled "The Linnean species as a system" [7]. It should be clearly understood, however, that the author applied the concept of a "system" to the hierarchy of intraspecific systematic units, and never at any time in the sense of a "functional system" as it is now understood (see, for example, work [4]). The species - system of N. I. Vavilov is a theoretical and multiple construct [36].

The standard of a morphological polytypical species was introduced by the ichthyologist L. S. Berg [5] and it came to serve as the basis for later systems of the species developed by G. V. Nikol'skii [23, 24, 26] and N. V. Lebedev [17]. According to G. V. Nikol'skii [26], all of the intraspecies groupings from subspecies to a tentative form are not "a level of species formation." Their specific character lies within the limits of a common "elasticity" of the species as a whole. They are all reversible and they can merge one into the other, since in a broad sense all intraspecific variations are intermergible. In actual fact, all intraspecific groupings of whatever rank are devoid of reality in such

a treatment, and they become a series of embodiments of the "elastic" species. Their specific character is not immobilized, it is reversible. The loss of any one of them, consequently, is compensatable in principle. In the species system of G. V. Nikol'skii /7 there are no units that could be considered to be an elementary working unit. It is no accident that the major Theory of fish stock dynamics [25] does not even make an attempt to define the actual object that is being described. "Stock" [stado] and "population" [populyatsiya] are employed as synonyms without any definition, while the compounds "nonspawning population" [nerestovaya populyatsiya] and "commercial population" [promyslovaya populyatsiya] demonstrate the application of the term in a most indefinite sense.

This variant of the species system of N. V. Lebedev [17], is not an attempt to analyze the population structure of a species, despite the assertion of Yu. P. Altukhov [3]. This is a nomenclatural and taxonomic system. The frequent employment of the word "population" should not lead one astray, since it is understood to mean the general population [naselenie] of a species, subspecies, race, stock, or portion of a generation (in the case of the anchovy), or a particular size-age grouping (in the case of the vobla [Rutilus rutilus]). The author makes use of the criteria of self-reproduction as the criterion for the taxonomic rank of intraspecific groupings. But its usage is not consistant. Self-reproduction is regarded as a property of all of the units from species to stock and it is not clear why, under these circumstances, race is accorded the status of a primary taxon while stock is not. The rank criteria for intraspecific groupings have been established. We can guess that it is not determined by the nature and

features of a specific grouping, but by its size and by the presence of "free" categories: "If some population is discovered, which differs from other populations, while an even smaller but also self-reproducing population is discovered within it... [then] the larger population will be a race, while the smaller one will be a stock [stado]." The concepts of race and stock "...in principle do not differ. In this case there is a purely quantitative difference - the stock is smaller than the race [17, p. 15]." But then the "system" degenerates into a ranking of intraspecific groupings according to size, the location of geographic ranges, and the number of individual numbers. The system of N. V. Lebedev devotes particular attention to the primary units of the intraspecific structure - the "elementary population." These are, by definition, non-hereditary, temporary groupings. But it is specifically these units that the author considers as evolutionary units in his particular variant of the hypothesis of sympatric species formation. N. V. Lebedev considers "elementary populations" to be a widely distributed, if not a universal phenomenon in the fish world. It is clear from this that the hypothesis of sympatric divergence on the basis of "elementary populations" aspires to wide application.

The species systems of G. V. Nikol'skii and N. V. Lebedev reflect the original views of both regarding the evolutionary process. This is of interest in the present context in so far as it demonstrates the direct link that exists between the most generalized theories and fundamental practical problems. G. V. Nikol'skii considered species formation at the level of the species as a whole. It is not true that he denied the hereditary character of intraspecific groupings [3]. He /8 simply did not consider this circumstance significant, since he did not

associate species formation with any intraspecific groupings. Naturally, in G. V. Nikol'skii's system of constructs it was the species as a whole that remained in the spotlight. There is not even any room in it for some kind of intraspecific unit that would be sufficiently individualized and with sufficient specific identity to be a separate, independent object of economic exploitation. In contrast to this, N. V. Lebedev transfers species formation to the sub-population level of "elementary populations" and in his species system as well there are no units that could be considered to be independent objects of exploitation. Not a single one of the structural units of the species systems examined contains in its definition the features that are essential for "a unit of usable stock" (for exploitation).

Such a unit is the population [populyatisiya] - the central element in the population-biological conception of the species. According to the definition given by E. Mayr [19], the species is a reproductively isolated assembly of interbreeding populations. The population is a "reproductive community of organisms with a common gene pool [44]" and it is considered to be the elementary evolutionary unit.

The essence of the population concept is generally accepted; the definition of its central entity - the population - remains, however, a topic of endless discussion. A huge number of definitions have given birth to the illusion that the entity itself is vague; it has even been suggested that the concept of "population" be abondoned and that population terminology be replaced by deme terminology [15]. L. Jonckers [50] defined population as a multitude of organisms standing in certain positive relationships based on twelve specific

definitions. Of course, such a definition does not reflect the specific character of a population and it is applicable to the most diverse "multitudes of organisms." The causes of this terminological babel were not numerous and they are sufficiently clear. First of all, the term is widely employed in a general sense without any semantic charge ("the plankton population of the Black Sea" and "the sparrow population of city X"), which is sooner a problem of linguistic clarity, but not of terminology. In the second place, the word "population" [populyatsiya] is frequently employed to designate the species population [naselenie = inhabitants] of some particular region or to designate some groupings, the rank of which is unknown and often even unimportant in terms of its significance (summary in article [54]). A third source is the abundance of definitions given by various disciplines (ecology, genetics, morphology, systematics, cybernetics, and so on). The diversity of such definitions reflects, on the one hand, the particular interests of the investigators in question and, on the other hand, the huge range of the populations themselves. V. Grant [8] refused in principle to give a "general formal" definition of population "that would serve as a standard in all cases [p. 24]." Finally, the definitions of population in a strictly evolutionary and genetic sense are also considerably diverse [33, 37, 18, 19, 34, 22, /9
31, 44, and others].

Population is characterized by two fundamental properties, essential to every entity in that class: (1) stable self-reproduction and (2) a common gene pool. These properties are not strict concepts and they require elucidation. Stability in this case is understood to mean simply the absence of imminent limitation in temporal existence:

when the necessary conditions exist, the population can remain in existence for an unlimited period of time. The notion of "self-reproduction" is applied equally to populations, to a species as a whole, and to ecosystems up to and including the biosphere. It is therefore useful to explain that population is the minimum self-reproducing unit that does not contain other self-reproducing groupings within itself. We are not here concerned with the minimum number of individuals capable of sustaining their own existence, but with the minimum actually existing self-reproducing groups. A common gene pool is reflected in the equal possibility [probability] of any allele being included in the genotype of each individual of the population. This possibility may not be realized in an absolute manner. For example, recessive lethals in a homozygote state are incompatable with the survival of the individual (and there will be no such individuals in the population), but the very fact that there is some possibility of their appearing will regulate, through the selection of individuals, their frequency within the system - the population. The common gene pool at the same time makes the population a complete functional system. The equal chance for the inclusion of any allele of the gene pool in the genotype of any individual is NOT equivalent to panmixia, i.e. to absolutely random breeding [28]. Panmixia does not possess gradations, and any deviation from it is already non-random breeding - descrimination (which is commonly observed in natural populations). The common gene pool also emphasizes the fundamentality of the population.

And so the conceptual definition that includes the most essential and the most general properties is the following: every

specific entity in the class "population" is characterized by stable self-reproduction and by a common gene pool.

In many cases, other diverse properties enter into the general definition of population. Some of these, for example, designate the existence of a unique population range, while others do not. It is clear that every population is characterized by [limitation to] a definite space, so that it is redundant to introduce this concept into a general definition, just as the designation of specific morphological, ecological, genetic, and similar features is redundant [37]. In a general sense it is clear that two populations of a single species cannot occupy the same point of a multidimensional heterogenous space and be subject to monovectorial selection of equal intensity, and, consequently, they cannot be identical. The level of differentiation among populations, however, may range in extent from something undetectable by existing methods to the species. /10

Populations, like the biological species, are characterized not by distinctions, but primarily by isolation. Two intraspecific groupings that are not distinguishable in any of the properties employed for that purpose but which are reproductively isolated, will be full-fledged populations.

Populations, like the species, are diverse. Even within the limits of a single species they differ in the size of their geographical ranges, in their numbers, and in their structure - in all features, depending on their "age," on their isolation mechanisms, on the level of gene exchange with neighboring populations, and on the vector and intensity of selection. The diversity of species had already been noted by A. S. Semenov-Tyan-Shanskii [32] and, in even more detail, by

E. Mayr [18, 19], K. M Zavadskii [10], and others. The majority of the causes that have been identified for the diversity among species also characterize the diversity among populations. The diversity among populations gives impetus to their classification (which is useful), but also to a hierarchy of populations, which is not valid in principle. In spite of all their diversity, populations are equal. The construction of a hierarchy of populations is no better justified than a hierarchy of species. Both the one and the other can be an object for classification, but not for ranking. All populations are members of a single category and they have the same rank - that of population. Usually such hierarchies of populations are theoretical constructs: perhaps the sole example of a description of population systems that is based on natural material is to be found in the works of Yu. P. Altukhov [3, 39]. According to the conceptions of this author, the quite ecologically diverse species that he studied are differentiated into population systems (stock [stada]) consisting of sub-isolates that are specific in terms of heredity - elementary populations. But neither the hereditary character nor the elementary character of the subsystems identified have been proven [20, 21]. We can add that even the presence of genetically specific isolates cannot be considered as proven: the differences between them in allele frequency lie, on the whole, within the limits of sampling error. The claim that the groupings which, differ from each other in gene frequency are reproductive isolates [3, p. 189] is true only when certain conditions exist, and the author has not demonstrated their existence. Considering the biology of the ocean perch, particularly the specific character of its reproduction, it is difficult to admit the existence

of a larger number of reproductive isolates within the confines of the Newfoundland Grand Banks and the Flemish Cape banks. To this we can add doubt about the nonspecific relationship of the samples, which increases as the distribution of Sebastes mentella and S. fasciatus in the regions under consideration becomes clearer [57].

The fundamental property of a population - its independent, stable self-reproduction - provides a basis for defining the population as the elementary "unit stock" [edinitsa zapasa] espcially in marine fishing. The basic properties of a population are given either /11 implicitly or explicitly in most of the definitions of a "unit stock" [58, 56, 62, 42, 49, 53, and so on]. It has been suggested that the term "unit stock" be substituted for the term "population" [56], and such a substitution does occur. Soviet literature often employs the concept of "stock" [stado] as an equivalent of "unit stock." This is a vague concept. N. V. Lebedev [17], for example, considers the stock [stado] to be the smallest self-reproducing unit, and K. P. Yanulov [38] subdivides it into "individual small biological units - populations [populyatsii]." There are many other definitions. In variations that correspond in content with the concept of "population" [populyatsiya], preference should be given to the general biological term "population" [populyatsiya].

The numerous attempts to give a special definition to "unit stock" are also related to the non-operational character of the conceptual definition of population. Such definitions contain only the general and essential properties of the entities and "do not work." The judgement about the existence of these properties is based on certain features which enter into the working definition. But every definition

that is based on features will only be partial and may not be adequate for a portion of the members of the class under consideration. It is impossible to give an enumeration of all of the features in which the necessary properties of the population appear in all the fish, since there is no universal "working" definition of population or "unit stock." The reproductive isolation of a population, for example, may show up in the separation of regions or of their periods of spawning or in both at once. These features are not absolute, since in any one of the given variants a mixture of the eggs and young is theoretically possible without subsequent differentiation based on the places (periods) of spawning.

The diversity of features in which the fundamental properties of the populations can make their appearance renders it possible to conduct research by many different methods. The adequacy of the features in relation to the properties can differ, and consequently the "decisive capacity" and the reliability of the different methods is not uniform.

Population studies on the primary commercial species of marine fish are further complicated by some common characteristics that they share. In the majority of cases these are pelagic (pelagobenthic) species for which the following are characteristic: (a) high numbers, frequently subject to sharp variations; (b) compact distribution over wide expanses; (c) pelagic eggs, which are often, as a rule, planktotrophic larvae; (d) significant ontogenetic and seasonal (cyclic) migrations, and functionally divided population ranges with spatial differentiation of size and age groupings; and (e) overlapping

population ranges (Clupeidae, Gadidae, Carangidae, Scombridae, and Scorpaenidae).

Evaluations of the size of stocks, recruitment, mortality, and /12
the size of the permissible removal - without which rational fishing is unthinkable - make sense only in so far as they estimate a concrete population. The same is true of forecasting commercial fishing. Clearly, the role of population studies in marine fishing is growing.

Accumulated practical experience in population studies in the fishing industry makes it possible to evaluate the domain and prospects for applying various methods of identifying populations (see, for example, article [49]). Below, we will briefly review some of the aspects involved in applying individual methods that are not touched upon by the authors, but which are of some practical interest.

Population parameters - size and age composition, growth rate, recruitment rate, mortality indices of numbers, the sex ratio and a number of others - can be distinguished in different populations and are frequently used to isolate them. There is, however, a widespread conviction that differences in samples based on these parameters, which indicate population subdivisions, are in many cases invalid. In particular, this applies to species of great longevity and of complex functional range structure in which local differences in any of the parameters mentioned can be intrapopulational. This is obvious in the case of differences in size and age composition. The growth rate that is defined (a) on the basis of samples from reproductive and spawning regions and (b) from regions inhabited by individuals of the same population but of different ages can differ fundamentally due to the existence of a relationship between the rate of growth, the age

(length) of sexual maturation, and the individuals' length of life [25]. The extended process of sexual maturation in fish is in general directly proportional to the average life expectancy at both the species and the population levels. The rate of growth of sexually mature and immature fish of the same age is different because of different metabolic structure (the presence or absence of generative components). Consequently, indices of the rate of sexual maturation, when they are calculated on the basis of samples from a single population that differ in the proportions of sexually mature and immature individuals, can be very different.

Mortality indices (more accurately, loss indices) for various regions of a population's range, with spatial differentiation by size and age will, of necessity be different.

The ratio of the sexes differs greatly in different species and in populations of a single species, while within the limits of a concrete population it can change with age or as a result of the spatial and temporal differentiation of individuals by sex. It is often no simple matter to determine the true ratio of the sexes and the size-sex (size-age) structure of the population. An example of the /13
unsuccessful utilization in samples of the sex ratio in the capacity of a "population parameter" occurs in the case of the ocean perch, a species with an established spatial differentiation by sex, can be found in Yu. P. Altukhov [3].

The index of local overfishing (a reduction of the catch in terms of effort expended and of the average length of the fish) is often regarded as an index of intraspecific differentiation. Clearly, the symptoms of local overfishing can appear in any instance when the

rate of removal is greater than the rate of recruitment (migration) in a specific region and within the limits of a single population. Subsequent observations in such cases show a reduction in the initial indices at a rate greater than the reduction in reproductively independent groupings. Data on the "overfishing" of rock grenadier in the northwestern Atlantic [29, 30] may serve as an example.

The determination of population parameters makes sense only in so far as they are given for the population as a whole and only in cases in which they are suitable for its identification. Populations, as a rule, possess different parameters (although this, in theory, is not compulsory), but it does not follow from this that groupings which differ from each other in the features mentioned are therefore populations. Populations, particularly those characterized by extensive range, with diverse environments and a complex functional subdivision, are in fact heterogenous in terms of the features mentioned.

Morphological features have been used longer than any others in order to study the structure of a species. The effacacity of their employment, however, has received mixed evaluations. Their hereditivity varies considerably [27, 11, 45] and has been poorly reseached. The influence of the environment can be very great [41]. Numerous instances of intrapopulational differentiation on the basis of morphological features have been described [41, 40, 61, 55, and so on]. Cases are also known in which there are no clear differences between populations that are otherwise known to be different. In general, we can conclude that the adequacy with which the fundamental properties of a population are reflected in morphological features varies greatly,

and the reliability with these features can be used under such circumstances remains doubtful. We can also add that morphological studies often accept the morphological shape of isolated samples, while morphological descriptions that characterize populations over the courses of their entire life cycle and throughout their entire range are rare.

Genetic and biochemical methods occupy a special place in research into the structure of a species and they have been acclaimed as the most accurate and the most promising in population studies of commercial marine fish [49, etc.]. It thus becomes all the more important to note that the interpretation of differences in frequencies of electrophoretic variants (phenotypes) and alleles found in samples /14 faces a vast array of limitations. On no account can we accept the claim that a statistically significant difference in allele frequencies in samples indicates that they belong to different populations [3, 6, and many other works]. There is a large corpus of data pointing to the non-random distribution of individuals that differ genetically within the limits of a population range. This has been pointed out by E. Meyer [18]. A classic example of this kind is the study on the American eel, Anguilla rostrata [51]. Similar data were obtained for the rock grenadier [2, 1] and the Peruvian jack mackerel [12] and for the article by L. I. Koval' (in this collection) entitled "Intra-specific differentiation in the jack mackerel Trachurus symmetricus murphyi by esterase phenotypes". A significant intrapopulational variability has been established in a great number of cases from year to year, from season to season, and from group to group [e.g., 43, 47, 56, 52 and so on]. The different components of populations having extensive and heterogenous ranges may be subjected to selection that

differs in intensity and direction (eel, grenadier). Different generations can become differentiated as a result of year-to-year differences in developmental conditions in the early stages of ontogeny [60]. Furthermore, the intrapopulational differentiation of genotypes by sub-niche is postulated by the distributional hypotheses of habitat selection [vibor nish] in different variants [9, 59]. There are no theoretical assumptions, logical grounds, or factual data that allow us to consider populations as being homogeneous on the basis of the features that we have reviewed. Contrary assertions are often argued by the achievement of a Hardy - Weinberg equilibrium in samples from natural populations. The area in which this law applies should be clearly understood. It postulates the constancy of allele frequencies in a population, given panmictic conditions and the absence of selection, mutation and differential migration. This law, however, does not maintain that the equilibrium of frequencies in a sample indicate that the four above mentioned conditions have been met. We know that the Hardy - Weinberg equilibrium is decided in terms of autosomal alleles in the very first mating, independent of the distribution and frequencies of alleles in the parents. Furthermore, a great many cases have been recorded of nonequilibrium distribution in natural populations with both an excess and a deficit of heterozygotes. Deviations from equilibrium can be constant, or they can be related to seasonal cycles [16, 35], or correlate with the size and age of the individuals. A surplus of heterozygotes is usually considered to be a manifestation of monogenic heterosis; a deficit is explained by the Valund effect [transliterated from Russian - perhaps Walund or some similar spelling - Tr.], even when it is essentially more than what is permissible from that point of view.

It can be stated that many results of genetic and biochemical studies have been far from clear and unambiguous, as had been assumed in the initial period of utilizing electrophoretic methods for marine /15
fishing research. The results of even the very reliable studies can often be treated with equal justification on the levels of both intrapopulational and interpopulational differences. It is obvious that in many cases it is not at all possible to treat genetic and biochemical methods as "absolute." It should be understood that it does not necessarily follow from this that their application is not promising. The electrophoretic method is unquestionably the most reliable of all the existing frequency methods of population study.

Furthermore, all of the frequency methods for differentiating populations that we have considered above share common theoretical limitations. The treatment of the differences that have been discovered as intrapopulational or interpopulational is not determined by the differences themselves. All of these methods result in a logical circularity, the essence of which is found in the following. A similarity between any of the indices that we have considered is no proof of their identity. Only differences are significant for the differentiation of populations. But differences can be intrapopulational, so that their interpretation requires a knowledge of whether the samples belong to a single population or to different populations, which is at the same time the purpose of the investigation. The description of populations for the purpose of isolating them requires a preliminary division, which is necessary for a correct description. This paradoxical situation can result in objections, but in practical research the latter operation is frequently employed: a preliminary

division for the sake of a subsequent correct description and a final division. The treatment of genetic differences between local groupings of eel expressly as intrapopulational did not follow from the nature and the degree of these differences, but was based upon the well-known fact of population unity. If not for this, who knows how many "populations" would have been found. The logical circle in which the investigator often finds himself is broken by the introduction of a hypothesis with a broader foundation. Usually this consists of at least general information on the life cycle of the object of investigation and the functional structure of its range, including an analysis of possible integrating and differentiating factors (the drift of plankton stocks, active migrations, and so on). Broad specialized studies of the population structure of commercial fisheries research targets are often time-consuming, laborious, and expensive. It is therefore all the more important to conduct such studies, in the first instance, in situations when there are already well-founded hypotheses regarding the division of the total stocks. The minimum basis for such a hypothesis is the existence in the groupings being studied of functionally valuable ranges with their own reproductive and spawning areas and all phases of the life cycle (all ontogenic stages).

In conclusion we shall note that the determination of a population as an elementary production unit and as a stock unit reflects, on the one hand, its relative dependence on other populations of the species; on the other hand, the determination is a relection of the transient stage of description and control at the level of a single species. Naturally the production indices of the population are determined within its ecosystem, which is the actual unit of /16

exploitation. With the transition to multispecific control the first step will have been taken to ecosystem management, where the role of population studies is increasing significantly.

CONCLUSIONS

1. No units in the nomenclature and taxonomic species system among fishes are characterized by the properties of a "unit stock." Such properties are only possessed by the population - a self-reproducing grouping with a common gene pool.

2. Just like the bilogical species, populations are characterized not by their distinctions, but by their isolation.

3. The general biological term "population" [populyatsiya] should be preferred to such concepts as "unit stock" [edinitsa zapasa] and "stock" [stado], which do not have a strict definition.

4. The reliability of the different methods of identifying populations varies, and it depends on the level of adequacy of the features utilized by the method, which reflect the fundamental properties of the population - reproductive isolation and a common gene pool.

5. No single frequency method of identifying populations contains within itself the criteria necessary for treating sampling differences as either intrapopulational or interpopulational, and therefore cannot be absolute.

6. Frequency methods are effective on condition that they are applied within the framework of more general hypotheses of population unity or division, which are assumed a priori in relation to the

frequency methods. Such a hypothesis must include facts or well-founded propositions regarding the existence of only one, or else two or more spatial or temporal groupings with functionally valuable ranges (the existence of reproductive and spawning areas and of all stages of the life cycle).

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